

SPIDERS ON RED SPRUCE FOLIAGE IN NORTHERN MAINE¹

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ABSTRACT

Spiders of 10 families, 16 genera, and at least 21 species were collected from foliage of *Picea rubens* Sarg. in northern Maine. Foliage samples were collected from tree crowns using an extendable pole pruner. Of 157 individuals, erigonids were numerically dominant (36%), followed by philodromids (18%) and salticids (15%). Mean spider densities/m² of foliage area were nonsignificant among sampling sites, but significantly more ($P = 0.05$) spiders were collected during the second sampling period (24-25 July) than during the first sampling period (7-8 June). Differences in spider densities between sampling periods were attributed to 1) seasonal activities and reproductive cycles of individual species, 2) weather during collection of foliage samples, and 3) two sampling methods (i.e., pole pruner with clamping device or pole pruner with catchment basket). Spider-budworm relationships and spider-habitat associations are discussed.

INTRODUCTION

Spiders are among the dominant predatory arthropods in forest ecosystems. In northeastern spruce-fir forests, spider densities are estimated to range from about 75,000/acre (187,500/hectare) (Morris 1963) to 125,000/acre (312,500/hectare) (Haynes and Sisojevic 1966a). Despite common occurrence and relative abundance of spiders, little is known about the arboreal spider fauna of coniferous tree species. Jennings (1976) summarized spider-faunal studies of North American trees; only nine species of conifers were included. Recent faunistic studies include spiders on balsam fir, *Abies balsamea* (L.) Mill., in New Brunswick (Renault and Miller 1972); on white fir, *Abies concolor* (Gord. and Glend.) Lindl. ex Hildebr., in California (Dahlsten et al. 1977) and in Oregon (Mason and Torgersen 1983); and on red pine, *Pinus resinosa* Ait., white spruce, *Picea glauca* (Moench) Voss, and white cedar, *Thuja occidentalis* L., in Minnesota (Stratton et al. 1979).

¹Mention of a commercial or proprietary product does not constitute endorsement by the U.S. Department of Agriculture, the Forest Service, or the University of Maine.

During our studies of the spruce budworm, *Choristoneura fumiferana* (Clem.), in northern Maine (Collins 1985), we sampled budworms and spiders on foliage of 160 red spruce, *Picea rubens* Sarg., trees. This paper reports spider species composition on red spruce foliage, compares relative abundances and densities during two sampling periods, and evaluates two sampling methods for arboreal spiders.

METHODS

Study Area.—The study area was located on Great Northern Paper Company lands about 60 km northwest of Millinocket, Piscataquis County, Maine. Individual study sites (8) were located along the eastern edge of Township 4, Range 12, WELS (45°58' North; 69°13' West), about 2.6 km east of Ripogenus Pond, and 2.5 km northwest of Soubunge Mt. (USGS, Harrington Lake Quadrangle, 1954). Elevations were about 335 m.

Five strip clearcuts were chosen for study in a spruce-fir forest infested with the spruce budworm. The strip clearcuts consisted of alternating uncut residual stands and clearcut strips from which trees had been harvested in 1977. The strips were oriented east-west, $\bar{x} = 94^\circ$, range 90-96°. The study area had been sprayed by the Maine Forest Service with Seven-4-oil® for spruce budworm suppression in 1981. No further chemical-insecticide treatments were made, including the study year of 1984.

Forest-Stand Characteristics.—Forest-stand parameters were measured on 16 variable-size plots established along the north and south edges of uncut residual strips (Fig. 1): two plots at each of eight study sites (A, B, C...H). Within each plot, a species inventory was taken of all trees ≥ 1.0 cm in diameter at breast height (dbh). Tree heights of three dominant or codominant softwoods were measured (m) on each plot with a Haga® altimeter. Stand ages were determined from tree increment cores ($n = 48$).

Foliage Samples.—Spruce budworm and spider populations were estimated during two sampling periods. The first sampling, 7 and 8 June 1984, corresponded with the budworm's L₃-L₄ larval stages; the second sampling, 24 and 25 July 1984, corresponded with the budworm's pupal stage. Within each plot, 10 dominant or codominant red spruce were selected for sampling. Trees were flagged and numbered so that the same trees could be used for both population estimates.

For the first sampling, we used an extendable pole pruner equipped with a clamping device (Stein 1969) to prune two midcrown branches (≥ 45 cm) from each tree. The clamping device holds the branch after it has been severed from the tree. Pruned branches were lowered or dropped to a ground cloth (3.6 x 3.6 m). All loose larvae and spiders were collected and preserved in vials containing 75% ethanol. Branches, associated vials, and labels were placed in clear plastic bags (30 x 61 cm) and transported to the laboratory for examination.

The same procedure and sampling intensity were followed for the second sampling, except that the pole pruner was equipped with a metal hoop and fine mesh net (16 x 18 mesh, 46 cm diam, 69 cm deep) which formed a basket beneath the cutting head of the pruner. Severed branches and any dislodged insects or spiders were caught in the basket and lowered to the ground by disassembling the poles.

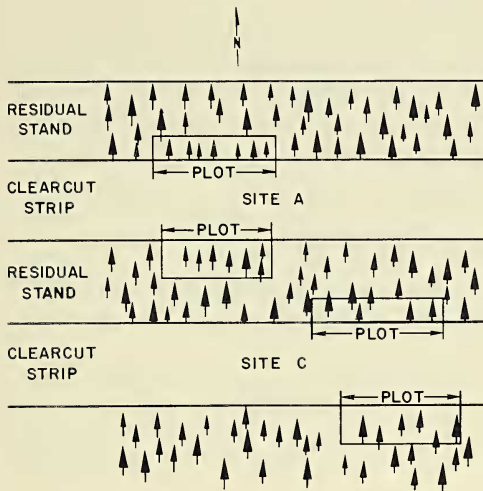


Fig. 1.—Schematic of strip clearcut spruce-fir forest showing residual stands, clearcut strips, variable plot sizes (16), and two of eight sampling sites (A, B, C . . . H), Piscataquis County, Maine.

In the laboratory, branches were stored in a walk-in cooler (3-4°C) until examined. All branches were examined by trained technicians within two weeks of collection. Foliated branch lengths and widths were measured (cm) and branch areas (A) calculated by the formula: $A = \text{length} \times \text{width} / 2$ (Sanders 1980). Each branch was cut into small, easily handled pieces (10-15 cm) with hand pruners. The pieces were then examined carefully for spruce budworms and spiders. All spiders were preserved in vials containing 75% ethanol. Population densities were expressed as budworm larvae-pupae and spiders per m^2 of branch foliage area. Sample sizes were: 2 branches/tree \times 10 trees/plot \times 16 plots (2/site) = 320 branches/sampling period, and 640 branches total.

Weather.—Because weather affects spider activity, temperature and rainfall data were obtained from the Great Northern Paper Company's weather station maintained at Ripogenus Dam, about 12.2 km SSE of the study area (NOAA, Climatological Data, New England, vol. 96 (6,7), 1984).

Spider Identifications.—Most of the spiders were identified with the identification keys and species descriptions of Kaston (1981). Additional consulted sources were: Chamberlin and Gertsch (1958) for the dictynids; Levi (1957) for the theridiids; Dondale (1959) for the erigonids; Berman and Levi (1971) and Levi (1974, 1977) for the araneids; Dondale and Redner (1982) for the clubionids; Dondale and Redner (1978) for the philodromids and thomisids; and Kaston (1973) for species of *Metaphidippus*. Following Platnick and Shadab (1981), we considered *Poecilochroa* a synonym of *Sergiolus*.

Because species descriptions are based chiefly on the genitalia, only sexually mature spiders were identified to species. Juvenile and penultimate stages were identified to generic level only, except for those of *Philodromus*, which were assigned to one of three species groups (*rufus*, *aureolus*, or *histrion*) based on color patterns of the legs, carapace, and abdomen (Dondale 1961a; Dondale and Redner 1968, 1975). Representative specimens of all identified species are deposited in the arachnid collection, U.S. National Museum, Washington, DC.

Data Analyses.—Because the observed spider densities were not distributed normally (Figs. 2 and 3) and variances were nonhomogenous (Hartley's test), even after transformations, we used nonparametric statistics for most analyses. The

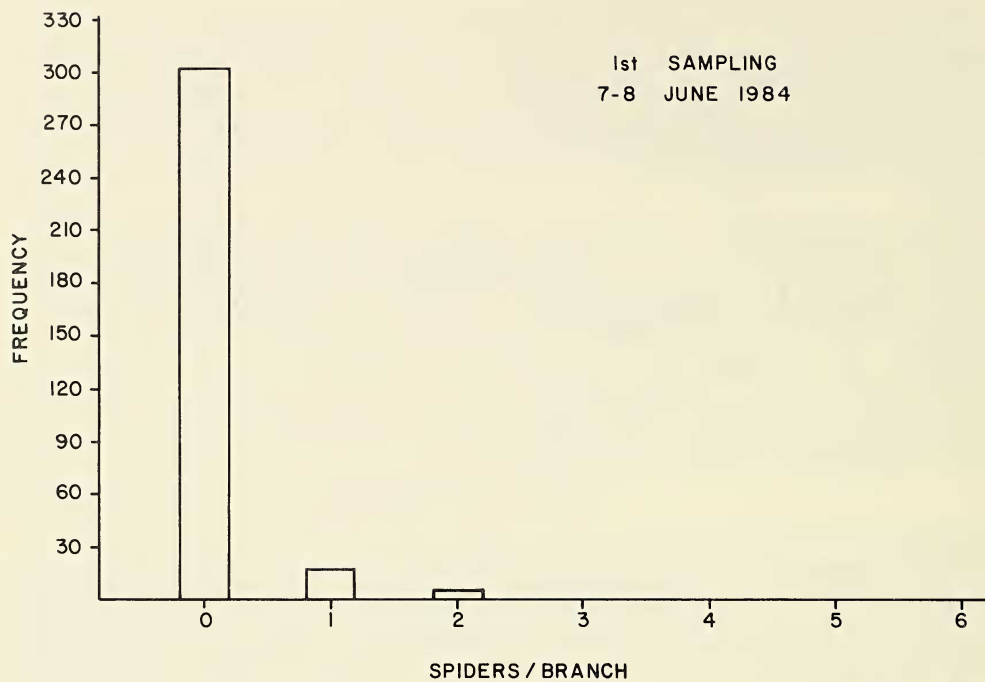


Fig. 2.—Frequency distribution of spiders on red spruce foliage, first sampling, 7-8 June 1984, Piscataquis County, Maine.

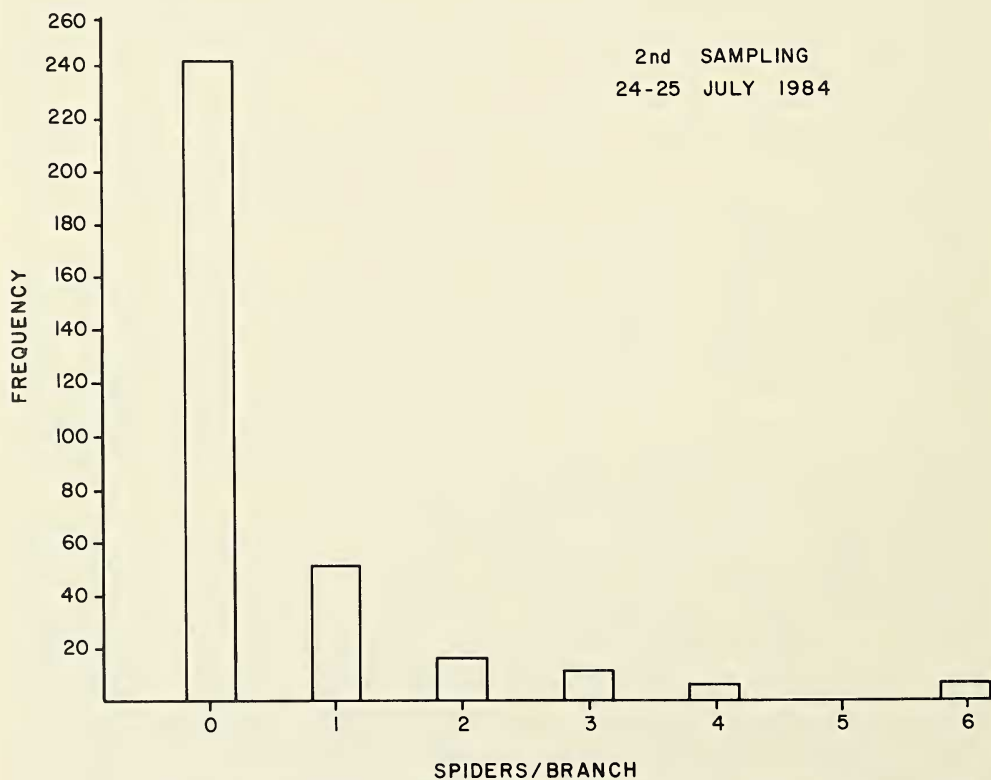


Fig. 3.—Frequency distribution of spiders on red spruce foliage, second sampling, 24-25 July 1984, Piscataquis County, Maine.

STP procedure (Sokal and Rohlf 1981) for multiple comparisons, based on the Mann-Whitney U-test, was used to compare spider densities among sites within sampling periods ($P = 0.05$). The Wilcoxon 2-sample test was used to compare densities between sampling periods for individual sites ($P = 0.05$) and over all sites ($P = 0.01$). Likewise, the Wilcoxon 2-sample test was used to test the independence of distributions between spider foraging groups (web spinners, hunters) ($P = 0.05$), and to compare spider densities between aspects (N, S exposure) over all sites ($P = 0.05$). Simple linear regressions were used to test for possible relationships between spider densities (dependent variable) and spruce budworm densities (independent variable), where $R^2 =$ coefficient of determination.

To estimate absolute populations, we converted spider densities per m^2 of foliage area to densities per ha (hectare) by the method of Morris (1955). Populations were computed as:

$$\text{spiders/ha} = \bar{x} \text{ spiders/m}^2 \text{ of foliage} \cdot \left(\sum_{sp=1}^N \text{BSA}_{sp} \right), \text{ where}$$

$\sum \text{BSA}_{sp}$ = sum of branch surface areas of spruce. The following equation was used to calculate branch surface area per tree: $\text{BSA}_{sp} = 2.64 + 3.34 \text{ dbh}_{cm}$, after Dimond (unpublished data).

RESULTS AND DISCUSSION

Forest Stands.—Species composition by percent basal area (m^2/ha) indicated a predominantly softwood component of red spruce (69.5%); northern white cedar (11.6%); white spruce (10.2%); white pine, *Pinus strobus* L. (2.7%); and balsam fir (4.6%). The hardwood component was composed of paper birch, *Betula papyrifera* Marsh. (1.5%), and red maple, *Acer rubrum* L. (<0.1%).

Red spruce trees averaged 13.7 ± 0.3 cm dbh and 12.4 ± 0.4 m height. Mean stand age was 62.1 ± 1.5 years.

Spruce Budworm Densities.—Mean larval and pupal densities per m^2 of foliage area were: L_3 - L_4 \bar{x} 's = 27.2 ± 2.6 over all sites, range 7.9 ± 2.1 to 39.4 ± 9.1 among sites; pupal \bar{x} 's = 5.4 ± 0.6 over all sites, range 3.3 ± 1.3 to 8.0 ± 2.2 among sites. As expected, larval densities were significantly greater ($P = 0.05$) than pupal densities among sites and over all sites (Collins 1985). No doubt, some of the age-interval mortality between budworm larval and pupal stages was due to spider predation; however, predation by spiders was not measured in this study.

Spider Species Composition.—Spiders of 10 families, 16 genera, and at least 21 species were collected from foliage of red spruce in northern Maine (Table 1). Of the 157 individuals collected, more were web spinners (54%) than hunters (46%). More species of hunters (12) were collected than web spinners (9); however, the same number of genera (8) were represented in each spider group. The erigonids were numerically dominant (36%), followed by the philodromids (18%) and the salticids (15%). Each of the remaining families accounted for fewer than 10% of the total individuals.

Table 1.—Spiders on red spruce foliage, Piscataquis County, Maine.

Family, <i>Species</i>	1st Sampling			2nd Sampling			Σ	%
	J	M	F	J	M	F		
WEB SPINNERS								
Dictynidae							4	2.5
<i>Dictyna brevitarsus</i> Emerton						1		
<i>Dictyna</i> sp.				3				
Theridiidae							4	2.5
<i>Theridion montanum</i> Emerton						3		
<i>Theridion murarium</i> Emerton						1		
Linyphiidae							10	6.4
<i>Pityohyphantes costatus</i> (Hentz)			1			4		
<i>Pityohyphantes</i> sp.				5				
Erigonidae							56	35.7
<i>Grammonota angusta</i> Dondale		1	2		1	11		
<i>Grammonota</i> sp.				41				
Araneidae							11	7.0
<i>Eustala anastera</i> (Walckenaer)						1		
<i>Eustala</i> sp.				1				
<i>Neoscona arabesca</i> (Walckenaer)						1		
<i>Araneus</i> sp.				5				
<i>Araniella displicata</i> (Hentz)						1		
<i>Araniella</i> sp.			2					
Subtotals		1	3	57	1	23	85	54.1
HUNTERS								
Gnaphosidae							2	1.3
<i>Haplodrassus</i> sp.				1				
<i>Sergiolus</i> sp.				1				
Clubionidae							3	1.9
<i>Clubiona canadensis</i> Emerton						1		
<i>Clubiona</i> sp.				2				
Philodromidae							29	18.5
<i>Philodromus exilis</i> Banks			1			1		
<i>Philodromus placidus</i> Banks						2		
<i>Philodromus</i> sp. (<i>rufus</i> grp.)	2			12				
<i>Philodromus</i> sp. (<i>aureolus</i> grp.)	1			6				
<i>Philodromus</i> sp. (<i>histrion</i> grp.)				4				
Thomisidae							15	9.6
<i>Misumena vatia</i> (Clerck)		1						
<i>Xysticus discursans</i> Keyserling						1		
<i>Xysticus punctatus</i> Keyserling			1					
<i>Xysticus</i> sp.	4			8				
Salticidae							23	14.6
<i>Salticus scenicus</i> (Linnaeus)			1					
<i>Metaphidippus flavipedes</i> (G. & E. Peckham)		1	1		1	2		
<i>Metaphidippus</i> sp.	2			15				
Subtotals	9	2	4	49	1	7	72	45.9
Totals	9	3	7	106	2	30	157	100.0

Web spinners were represented by only two families, two genera, and two species in the first sampling; this compares with five families, eight genera, and nine species in the second sampling. Hunting spiders were represented by three families, five genera, and six species in the first sampling; this compares with five families, six genera, and nine species in the second sampling. Combining web spinner and hunter groups, the number of taxa doubled between sampling periods; i.e., five families, seven genera, and eight species in the first, and 10 families, 14 genera, and 18 species in the second.

Juveniles of the *Philodromus rufus* group (Table 1) likely represent both *P. exilis* Banks and *P. placidus* Banks; juveniles of the *aureolus* group probably are *P. pernix* Blackwall, a common inhabitant of coniferous foliage. Juveniles of the *histrion* group are most likely *P. mysticus* Dondale and Redner, a species collected from black spruce, *Picea mariana* (Mill.) B.S.P., from white spruce, and from balsam fir (Dondale and Redner 1975).

Spider Age and Sex Ratios.—The ratio of juvenile to adult spiders was 0.9 for the first sampling and 3.3 for the second sampling. The ratio of males to females was 0.4 for the first sampling and 0.1 for the second sampling. Seasonal activities and reproductive cycles may account for some of these differences in life stages between sampling periods. For example, some arboreal species attain reproductive maturity and lay eggs that produce young spiderlings in midsummer to late summer (Dondale 1961b).

Spider Densities.—Only 5.3% of the 320 pruned branches had one or more spiders at the first sampling (Fig. 2). During the second sampling, 24.7% of the 320 pruned branches had one or more spiders (Fig. 3). The maximum number of individuals per branch was two during the first sampling, and six during the second sampling.

Frequency distributions between spider foraging groups (web spinners, hunters) were not significantly different ($P = 0.05$) by the Wilcoxon 2-sample test.

Mean densities of spiders per m^2 of foliage area ranged from 0.0 to 1.4 for the first sampling and from 1.5 to 16.6 for the second sampling (Table 2). None of these densities were significantly different ($P = 0.05$) among sites by the Mann-Whitney U-test, STP procedure (Sokal and Rohlf 1981). All sites showed increases in spider densities from the first to the second samplings; all but sites A, B, and D showed significantly greater densities by the Wilcoxon 2-sample test ($P = 0.05$) for the second sampling period. Between sampling periods, overall mean densities were significantly greater (Wilcoxon 2-sample test; $P = 0.05$) for the second sampling period (Table 2). Possible factors contributing to these differences were: 1) seasonal activities and reproductive cycles of the various species, 2) weather during field collection of branch samples, and 3) sampling methods.

We observed 92% more juveniles and 69% more adults during the second sampling than during the first sampling. No doubt, some of these differences can be attributed to the reproductive cycles of individual species and the production of young spiderlings in midsummer. For example, *Pityohyphantes costatus* (Hentz) produces eggs in early July in Quebec (Manuel 1984); *Araniella displicata* (Hentz) reaches sexual maturity in May and June and produces eggs in early July in Connecticut (Kaston 1981). However, juveniles of biennial species should have been prevalent during both sampling periods. At least six of the species found on red spruce foliage, *Theridion murarium* Emerton, *Araniella displicata*,

Table 2.—Spider densities on red spruce foliage, Piscataquis County, Maine ($n = 320$ branches/sampling). Column means within sampling periods are not significantly different by Mann-Whitney U-test, STP procedure (Sokal and Rohlf 1981), $P = 0.05$. Row means (a, b) followed by the same letter are not significantly different by Wilcoxon 2-sample test, $P = 0.05$. Overall means (x, y) are significantly different by Wilcoxon 2-sample test, $P < 0.01$.

Site	1st Sampling		2nd Sampling	
	\bar{x}/m^2	(\pm S.E.)	\bar{x}/m^2	(\pm S.E.)
A	1.17a	(0.58)	1.47a	(0.76)
B	0.40a	(0.40)	2.34a	(1.00)
C	0.89a	(0.64)	9.69b	(2.91)
D	1.39a	(0.81)	5.42a	(2.47)
E	0.00a	(0.00)	7.20b	(2.29)
F	1.27a	(0.64)	16.57b	(5.86)
G	0.74a	(0.55)	8.67b	(1.88)
H	0.26a	(0.26)	5.75b	(1.95)
Overall	0.76x	(0.18)	7.14y	(1.68)

Misumena vatia (Clerck), *Xysticus punctatus* Keyserling, *X. discursans* Keyserling, and *Philodromus placidus*, have biennial life histories (Dondale 1961b, 1976). Dondale (1961b, p. 785) noted that "biennialism is fairly prevalent among tree and shrub spiders of the North Temperate Zone." Juveniles of *Xysticus* and *Philodromus* were collected during both sampling periods but were more abundant during the second sampling. This suggests that weather or sampling method differences were important.

Mean daily temperatures were about the same for both sampling periods—17.2°C (7 June) and 20.8°C (8 June) for the first sampling, and 20.9°C (24 July) and 17.2°C (25 July) for the second sampling. About equal amounts of precipitation fell during both branch-collection periods, 1.6 cm (1st) and 1.1 cm (2nd). During the first sampling, most of the trees (sites A-F) were sampled when the foliage was dry; whereas, during the second sampling, most of the trees (sites A-E) were sampled when the foliage was wet. We suspect that spider activity may have been retarded during the second sampling due to the wet foliage, thereby increasing the probability of collection. Conversely, spider activity probably was not adversely affected by the clear, warm, and sunny weather during the first sampling, thus diminishing the probability of capture. Lowrie (1971) found that sweep-net catches of *Oxyopes* spiders were significantly greater in herbaceous vegetation when the dew was heavy.

The two sampling methods used in this study also may have contributed to the differences in spider densities between sampling periods. Some spiders may have been lost with either sampling method, i.e., a pole pruner equipped with a clamping device, or a pole pruner equipped with a basket. However, we suspect that spiders were dislodged more readily and lost without the catchment basket. Although Churcher (1981) showed there were no significant differences in budworm counts on red spruce foliage sampled with and without baskets in New Brunswick, spiders may be more susceptible to disturbance, particularly species that build their webs between branch apices. Because manipulation of a pole pruner equipped with a basket is difficult, adjacent branches often are brushed; this may add spiders to a branch sample. Both sampling methods need to be tested at the same time and place for spiders.

We found no significant difference in spider densities by aspect over all sites. Trees north (southerly exposed) and trees south (northerly exposed) of the clearcut strips had comparable populations per m² of foliage area; N tree \bar{x} 's = 0.48 ± 0.20 (1st sampling), 8.67 ± 1.71 (2nd sampling); S tree \bar{x} 's = 1.05 ± 0.33 (1st sampling), 5.60 ± 1.08 (2nd sampling). Although some individual sites varied, overall means within sampling periods were not significantly different between aspects by the Wilcoxon 2-sample test, $P = 0.05$.

Absolute population densities were estimated as 68,995 spiders/ha for the first sampling and 645,853 spiders/ha for the second sampling. The latter density is double that reported by Haynes and Sisojevic (1966a) for spiders in a balsam fir stand in northern New Brunswick. We suspect that spruce may support more spiders, both individuals and species, than fir. Stratton et al. (1979) found that white spruce had the highest number of individuals and species compared with red pine and white cedar in Minnesota.

Spider-Budworm Relationships.—Regression analyses indicated very weak correlations between spider and budworm densities on red spruce foliage; $R^2 = 0.004$ ($P = 0.28$) for the first sampling, and $R^2 = 0.018$ ($P = 0.02$) for the second sampling, where $n = 320$ branches each sampling period. More refined sampling techniques are needed to fully assess the density independent-dependent relationships between spiders and spruce budworms.

All life stages of the spruce budworm—eggs, larvae, pupae, and adults—are susceptible to predation by spiders. Some of the species found on red spruce foliage during this study have been observed in previous studies feeding on various stages of the spruce budworm. The salticid, *Metaphidippus flavipedes* (G. & E. Peckham), feeds on eggs and first instars (Jennings and Houseweart 1978). The web spinners, *Theridion murarium* and *Araniella displicata*, capture budworm moths in their webs (Jennings and Crawford 1985). In laboratory tests, *Grammonota angusta* Dondale readily captured and fed on second instars of the spruce budworm (Haynes and Sisojevic 1966b). *Dictyna phylax* Gertsch and Ivie, a species related to *D. brevitarsus* Emerton, caused considerable mortality to second instars of the spruce budworm on "stocked" balsam fir branches in New Brunswick (Renault and Miller 1972); survival of budworm larvae was only 3% on branches with *D. phylax* and 60% on branches without spiders.

Detailed serological studies of spider predation on the spruce budworm by Loughton et al. (1963) indicated that: 1) the erigonids, particularly *Grammonota pictilis* (= *G. angusta* according to Dondale (1959)), were the most important group because of their large numbers, 2) the theridiids were the most effective predators, based on percentages showing positive feedings on budworm, and 3) the salticids were important predators at all stages of larval development, including the late instars. Mortality during the late larval stage influences generation survival of the spruce budworm (Morris 1963). At low larval densities, Watt (1963) estimated that only 0.46 larvae/10 ft² (0.49 larvae/m²) of foliage would have to be eaten by predators, including spiders, to account for a decrease in population survival rate. Additional studies are needed to fully evaluate the predatory impact of red spruce spiders on spruce budworm populations, especially at low pest densities.

Spider Habitat Associations.—None of the species of spiders collected from red spruce foliage are restricted to that habitat; most of the adult species have been collected from two or more species of conifers (Jennings and Collins 1987). Our

collections of *Salticus scenicus* (Linnaeus), *Haplodrassus* sp., and *Sergiolus* sp. appear unusual because *S. scenicus* generally is associated with domestic habitats (Kaston 1981) and species of both gnaphosid genera generally are ground dwellers (Platnick and Shadab 1975; Kaston 1981). However, *S. scenicus* has been collected from loblolly pine, *Pinus taeda* L., in Oklahoma (Bosworth et al. 1971); *Haplodrassus* sp. from shortleaf pine, *Pinus echinata* Mill., and loblolly pine in Arkansas (Peck et al. 1971); *Poecilochroa* sp. from white fir in Oregon (Mason and Torgersen 1983) and from shortleaf and loblolly pines in Arkansas (Peck et al. 1971); and *P. montana* Emerton from Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, in British Columbia (Turnbull 1956).

The crab spider *Misumena vatia* frequently is collected from flowering shrubs and forbs; however, it has also been taken from several conifer species (Jennings and Collins 1987). Collections of *Xysticus discursans* usually are made by pitfall traps and sweep nets in both grassland and wooded areas (Dondale and Redner 1978); our collections of this and other spider species from red spruce foliage represent new, previously unknown habitat associations.

The remaining species of spiders found on red spruce foliage are arboreal in habit; however, none are restricted to trees and to conifers. Some, e.g., *Philodromus placidus* and *Xysticus punctatus*, are more frequently collected from coniferous trees than from deciduous trees.

CONCLUSIONS

With conventional budworm sampling techniques, our results indicate a relatively sparse spider fauna (21 species) associated with red spruce foliage. No doubt other sampling methods (e.g., knockdown sprays, beating-cloth collections, destructive whole-tree samples) and sampling over a more extended period (e.g., April-October) would add additional species to the spider faunal list for red spruce. The objectives of this study were to sample spiders during only two restricted time periods of budworm development, L₃-L₄ larval stages and the pupal stage. With additional samplings, spider species composition, age, sex ratio, and density are all apt to change due to individual life histories, reproductive cycles, and seasonal activities. Conventional budworm sampling methods are useful for determining frequencies and densities of common associated spiders; however, these methods are inadequate for determining important predator-prey relationships. More refined sampling methods and direct or indirect methods of assessing predation are needed (e.g., serological techniques for detecting target-prey antigens or tagging potential prey with radioisotopes).

Our hypotheses regarding possible factors affecting spider densities (i.e., sampling methods, weather conditions during sampling, seasonal activities and reproductive cycles of individual spider species, and tree physiognomies) need further testing in independent studies with controlled conditions. Such studies may elucidate important spider-tree associations.

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